Biology of Ammophila evansi and A. mediata in Northern Michigan (Hymenoptera: Sphecidae)

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Abstract.—The sphecid wasps Ammophila evansi Menke and A. mediata Cresson were observed in the Huron Mountain region of Marquette County, Michigan. The eastern A. evansi is restricted to exposed rocky slopes, while the western A. mediata occupies level sand plains dominated by Pinus banksiana. Both species prey on arboreal caterpillars, utilizing one prey per one-celled nest. Both species are at the limits of their ranges in Michigan, but do not occupy the same habitats when they occur together.

Introduction

The genus Ammophila in North America has been relatively well studied ethologically (Evans 1959, 1965; Powell 1964; Parker et. al. 1980; Hager and Kurczewski 1985, 1986) and taxonomically (Menke 1965), but many gaps remain in our knowledge of the behavior of the majority of the species. For many taxa, all that is known is their recorded distribution from which some inferences can be made, such as the type of habitat in which they are likely to occur. Usually though, a mere label cannot impart the full spectrum of desirable data. A case in point is our study of Ammophila evansi Menke and A. mediata Cresson made at the Huron Mountain Club in northwestern Marquette County, Michigan.

A. mediata is a predominantly western montane and boreal Canadian species (Krombein 1979) reaching its easternmost U.S. distribution in northern Michigan (Fig. 1). A. evansi, however, is an eastern U.S. species reaching its westernmost distribution in the upper peninsula (UP) of Michigan (Fig. 1). Extensive collecting within the state has failed to yield any A. evansi specimens from the lower peninsula (LP). Were one to be guided by county records alone, it might seem that A. evansi and A. mediata are sympatric in the UP. However, upon closer inspection, we find that the two species are actually microallopatric in this region, differing greatly in their habitat preferences, which apparently do not overlap. These differences are detailed in the observations that follow.

Ammophila evansi

A. evansi was observed on exposed granitic outcrops on Breakfast Roll Mountain in full sunlight from 1400–1700 h on August 4, 1985, and briefly on June 27, 1986. Ambient temperature during the observation periods was 26°–28° C, and the surface

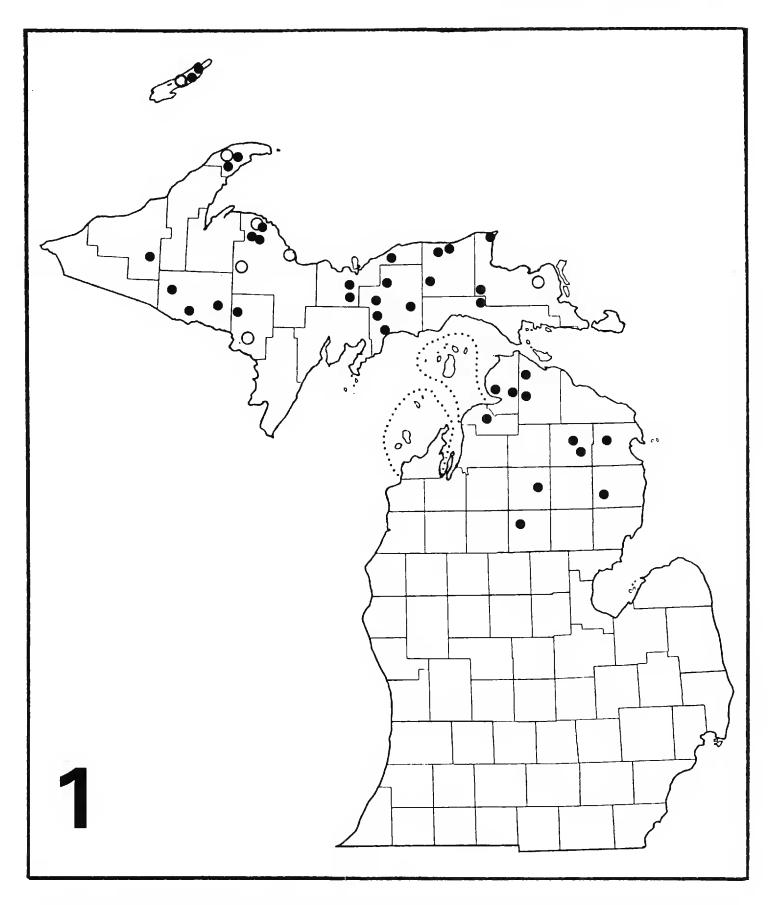


Figure 1. Map of Michigan, showing the distribution of *Ammophila evansi* and *A. mediata*. Open circles denote *evansi*; closed circles, *mediata*.

temperature of the rock was 30°-38° C. The rock outcrops ranged from 25 to 100 m above the flat areas of the Huron Mountain Club.

Males were seen flying 10–30 cm above the ground, and visiting flowers of *Solidago hispida*, which was flowering profusely on the rocky slopes in August, and *Rhus glabra* inflorescences in June. Even with a fairly stiff breeze, the males were quite active, flying from one flower clump to another, and searching for females.

A. evansi females were seen running over bare rock and sparsely vegetated, moss-covered rocks. Several females flew to low shrubs (Rhus sp.) and examined the branches before flying off, while others were seen obtaining nectar from S. hispida and R. glabra. The only female found nesting (85–2) had begun her nest closure at 1545 h. The nest was situated in a moss-covered depression surrounded by rock on a SE facing slope. The soil was very dry, sandy-organic, and quite dark. Making at least 14 trips to gather filler material from the immediate area, she filled the entrance, using some soil, but mostly pieces of dried moss, small twigs, and pieces of dead sumac leaves. Bits of organic debris used for fill were less than two times the diameter of her head. Most of the sand removed during the excavation of the burrow was scattered on the moss; thus she did not use much of it for fill. She did, however, fly up with one load of soil from what little tumulus was present, and dropped it on the moss away from the entrance. At 1607 h she flew off to feed on Solidago flowers, and returned three minutes later to pull a dry leaf over the burrow entrance, and then departed. She returned at 1615 h, searched briefly around the nest area, picked up small twigs of sumac, discarding them until she found one of the proper size, which she then dropped over the entrance. Appearing to be finished at 1620, she began to leave the area and was captured.

The nest of 85-2 was a typical "Ammophila-type"; a single cell at an oblique angle to the burrow. The dimensions were as follows: Entrance diameter = 1.0 cm, cell depth = 3.7 cm, with the cell 2.4 cm long \times 1.3 cm wide. The prey, a single large noctuid of the genus Zale, was curled up in the cell with the wasp's egg on the right side of the third abdominal segment. Four miltogrammine fly larvae were on the wasp's egg, which measured 3.0×0.6 mm. The flies were not reared.

Ammophila mediata

A. mediata was commonly encountered at the Huron Mountain Club, especially in flat, sandy areas dominated by Jack pine (*Pinus banksiana*) or near the Lake Superior shore at Conway Bay. Nesting areas were situated where the soil was sand to sand-gravel, friable, and not compacted or stony.

Based on hand collecting and Malaise trap catches from 1983 to 1985, A. mediata was the most common species of Ammophila at the Huron Mountain Club, accounting for 42% of the total (266 specimens), followed by A. urnaria Dahlbom (29%), A. azteca Cameron (25%) and A. evansi (4%). Since most Malaise traps were placed in open sandy areas, the catches may be somewhat biased towards A. mediata. No A. evansi were caught in the Malaise traps from these areas.

Several female A. mediata were observed hunting for arboreal caterpillars among the branches of Jack pines bordering the nesting areas. One wasp spent 15 min searching along the small branches and twigs of a Jack pine, flying up and down from branch to branch, and then walking along the length of the branches, tapping the bark with her antennae. Although prey capture was not seen, two females provisioned their nests with Zale sp. larvae (The "pine false-looper", family Noctuidae) that are mottled gray and brown and resemble the color of Jack pine branches, where they presumably were captured.

On Aug. 4, a female A. mediata (85–4) was excavating a nest at 2023 h at the edge of a depression along a powerline right-of-way. She brought out a load of sand every 15–20 s, and dropped it on the surface while flying up and away from the entrance. At

2046 h she temporarily closed the nest and left the site. The ambient temperature was 24°C.

On Aug. 5, we returned to the site of 85–4's nest and at 1059 h spotted the wasp carrying a large caterpillar back to the nest. The prey was carried in the usual ammophiline fashion (mandibles and mid-legs used to carry the prey venter-up). She stopped for 10 s, 1.5 m from the nest, dropped the prey amidst some dead branches and picked it up again. She resumed her trek to the nest, pausing for 2 s when 20 cm from the entrance. She then dropped the prey at the entrance, removed the temporary closure, went inside, and pulled the prey inside headfirst. She exited the nest 43 s later and began closure at 1108 h, finishing three minutes later.

The wasp used some sand during closure but mostly bits of organic debris, choosing pieces that were about the size of her head to fill the burrow. The fill was tamped in with her head, and then she removed any remaining tumulus.

On Aug. 6, a female (85–9) was caught carrying a geometrid larva along the powerline right-of-way at 1920 h. She had carried her prey in a straight line through several small brush piles for a distance of 16 m before being netted.

Wasp 85–17 was nesting at the edge of a sparsely vegetated area surrounded by patches of open sand in an old aspen clear-cut on Aug. 7. The nest site was adjacent to a stand of Jack pines, and aspens were regenerating in clones not far from the open sand. The wasp was first observed at 1600 h carrying her prey 6 m from the nest. Travelling in a straight line, she dropped her prey at the entrance, removed the closure, went inside, and then pulled the prey into the nest. The prey, a notodontid of the genus *Gluphisia*, feeds on poplars and willows (G. Godfrey, in litt.), suggesting that the wasp may have caught the prey within a short distance from the nest.

In a Jack pine forest on Aug. 8, another female (85–22) was seen carrying a Zale sp. larva at 1200 h, just prior to placing it in the nest. The nest was situated in a sloping edge of a sand-gravel road in an open sandy clearing bordered by pines. Because of the gravelly soil, the entrance was irregularly shaped. At 1201 h the wasp dropped her prey near the entrance, removed the temporary closure, went inside, and came out headfirst to pull the caterpillar inside. She took 84 s to oviposit and return to the entrance to start closure.

At 1600 h the same day, another female (85–28) was found clasping a large noctuid on a wave-thrown tree trunk about 20 m from the shore of Lake Superior (Conway Bay). The ambient temperature was 18°C. The wasp did not attempt to move when approached, and stayed motionless when attempts were made to disturb her. After walking for only a few cm with prey, the wasp and prey were taken for identification.

Wasp 86–3 was found digging her nest in loose sand near bracken fern and blueberries along the power line right-of-way at 1400 h on June 22. She walked backwards with each load of soil, dropping it 10–20 cm from the entrance. A load would be removed every 10–12 s. At 1414 h she made a temporary closure, filling the entrance with a small pebble, pieces of moss, and other organic debris; briefly oriented, and walked off. The burrow was checked at 2000 h, and again the next day. No provisioning had occurred. We theorize the wasp may have been captured in a nearby Malaise trap. Another wasp of this species (86–5) was observed at 1900 h, as she was carrying her geometrid prey back to the nest. After following a meandering route for 35–40 m in 12 min, she dropped the prey alongside the nest entrance at the periphery of a blueberry bush near a sand road. She removed the temporary closure,

went inside and pulled the prey into the burrow. She emerged 60 sec later to close the nest.

Wasp 86–7 was observed on June 23, near the aspen clear cut area. The wasp was first seen with her prey in a grass clump at 1300 h, and was dragging the caterpillar towards the entrance of her nest, 4 m away. A miltogrammine fly was stationed nearby, but apparently did not oviposit on the prey. The female emerged 40 sec after provisioning and ovipositing to complete final closure of the nest. Organic debris was mostly used to fill the burrow.

We observed one case of suspected nest usurpation. On June 23, at the aspen clear cut, a wasp (86–8) opened up a fully provisioned nest and removed the prey and late instar wasp larva, which she proceeded to discard to one side, as if removing debris from a closure. It is unknown if she was the originator of the nest. Unfortunately, we disturbed her and she did not return to the site.

Many male A. mediata were found flying close to the ground, and inspecting low shrubs in open sunlit areas of Jack pine woods near the aspen clear cut. One male approached a female from the rear, clasped her with his legs and mandibles (behind her head), and repeatedly stroked her abdomen from side to side with his. They remained coupled while still on the ground.

Table 1 lists all of the nest dimensions, egg placement, and species of prey from the *A. mediata* nests. No miltogrammine maggots were found on the prey. Three eggs (P85-4, 17, 22) each measured 3.0×0.6 mm.

Discussion

Although A. evansi and mediata appear sympatric at the Huron Mountain Club and in other areas of the UP, they are still microallopatric, due to their different habitat requirements. A. evansi, most often encountered in the eastern U.S., has been collected on rocky limestone outcrops (MFO pers. obs.), boulder-strewn ridges and river edges (Menke, in litt. 1985), and dry, rocky hillsides (M. Arduser, in litt. 1986). Thus, it is no surprise that its distribution in the UP corresponds to exposed rocky areas (Fig. 1). The paucity of these sites in the LP explains its absence there. Conversely, A. mediata is a western-montane and trans-boreal species that seems to be limited to flat sandy areas where conifers predominate. In Michigan, such areas are widespread in the UP and northern LP.

Although the two species are placed in the *azteca* species group (Menke 1965), they are quite similar in behavior to *A. urnaria* Dahlbom, (in the *urnaria* species group) in that they provision each nest with a single large caterpillar, rather than using multiple small caterpillars in the manner of *A. azteca* Cameron. Prey are transported on the ground due to their large size, rather than aerially, as with *azteca*. Due to the limited number of observations on *evansi*, it is premature to compare the behaviors of *evansi* and *mediata*.

Thus far, Michigan and Quebec (Finnamore 1982) are the only areas where the ranges of *mediata* and *evansi* are known to overlap, and the Huron Mountain area is the only locale where the species have been studied biologically. Observations on the behavior of each species at the other ends of their ranges could be compared to data from Michigan, to see if any displacement of behavior has occurred where they contact each other. Morphologically, *mediata* and *evansi* appear to be sibling species

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Table 1. Summary of Ammophila mediata nest data.

WASP	Entrance Diam. (mm)	Burrow Length (cm)	Cell Depth (cm)	Cell Size L×W(cm)	Egg ¹ Position	Prey
85-4 `	6.0	2.6	2.0	1.6×1.0	R-4	Melanolophia sp. (Geometridae)
85-9	_	_	_			Ectropis crepuscularia (D.&S.) (Geometridae)
35-17	8.0	2.5	1.8	1.2×1.0	L-4	Gluphisia sp. (Notodontidae)
35-22	12.0	4.2	3.5	2.6×1.3	L-3	Zale sp. (Noctuidae)
35-28	_	_			_	Zale sp.
36-5	6.0	3.2	3.7	1.8×0.6	L-4	Geometridae
86–7	6.0	2.4	2:7	1.5×0.7	L-4	Geometridae

¹Left (L) or right (R) side and abdominal segment number.

(see Menke 1965), and our behavioral observations point toward this direction as well. Future studies should consider this aspect when analyzing behavioral data.

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The wasps, prey, and associated field notes have been deposited in the University of Michigan Museum of Zoology.

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